TAXONOMIC STUDIES IN THE MICONIEAE (MELASTOMATACEAE). III. CLADISTIC ANALYSIS OF AXILLARY-FLOWERED TAXA[1]

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ABSTRACT

The axillary-flowered members of the Miconieae are hypothesized to be a monophyletic group, and the generic relationships within this group have been investigated by means of a preliminary cladistic analysis, which resulted in the following taxonomic conclusions. *Henriettea* is circumscribed broadly, including *Henriettella* and *Llewelynia*, as is *Loreya*, which is considered to include *Bellucia* and *Myriaspora*. The small genus *Kirkbridea* is likely the sister group of *Henriettea* sensu lato. *Clidemia* sect. *Calophysoides* and *Maieta* form a single clade and are considered congeneric. *Mecranium* (including *Ekmaniocharis*), *Killipia*, *Huilaea*, and the axillary-flowered 5- or 6-merous species of *Ossaea* all are considered generically distinct due to their isolated cladistic positions. Species of *Clidemia* sect. *Sagraea* along with *Necramium* and the axillary-flowered and 4-merous species of *Ossaea* are considered a distinct genus, *Sagraea*; an autapomorphy for this group was not consistently present in the generated cladograms, and the genus is considered metaphyletic. *Clidemia* sect. *Miconiopsis*, although usually considered axillary-flowered, actually has both terminal and axillary inflorescences and may be congeneric with *Miconia* (and likely is related closely to sect. *Tamonea*). Thus, axillary-flowered groups recognized at the generic level include: *Henriettea*, *Huilaea*, *Killipia*, *Kirkbridea*, *Loreya*, *Maieta*, *Mecranium*, *Pentossaea*, and *Sagraea*. Axillary-flowered Miconieae appear to form two major clades based primarily on the crystal type present in the leaf mesophyll and stem. Megastyloids (sometimes along with druses) occur in *Loreya*, *Kirkbridea*, and *Henriettea*, while only druses are found in the remaining genera. Cladistic relationships among the genera possessing only druse crystals are obscure, although *Huilaea* is probably basal within this complex, as reflected by its large flowers with well-developed pedicels, and *Sagraea* is likely most closely related to *Mecranium*, the two being linked by the synapomorphy of 4-merous flowers. Relationships of axillary-flowered taxa to those with terminal infloresences are discussed briefly.

The Miconieae Triana (Melastomataceae) are a diverse tribe of ca. 30 neotropical genera, including ca. 1,800 species. As discussed previously (Judd, 1986a), the genera within the tribe are poorly characterized, often difficult to discern, and defined quite arbitrarily (Cogniaux, 1891; Macbride, 1941; Gleason, 1932, 1958; Wurdack, 1972). In order to clarify relationships within this large and complex group, a preliminary cladistic analysis of the axillary-flowered taxa of Miconieae was conducted as reported here.

Within the Miconieae, the inflorescence may be either terminal or lateral. Plants with terminal inflorescences have hapaxanthic shoots in which the apical meristem of the shoot becomes wholly transformed into a flowering axis after a period of vegetative growth, while plants with axillary inflorescences have pleonanthic shoots in which the apical meristem continues its vegetative activity while producing lateral flowers or inflorescence axes (see Judd, 1986a; Weberling, 1988). Inflorescence position, along with the correlated characters of growth architecture, has been shown to be a valuable taxonomic character in the tribe and is usually uniform within sections or genera (Judd, 1986a).

The axillary-flowered condition is likely a derived state within the Miconieae because nearly all members of the Merianieae show terminal flowers. The latter tribe is a reasonable outgroup taxon considering possible tribal relationships suggested

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by J. Wurdack (Welle & Koek-Noorman, 1981). The same conclusion would be reached through the use of a generalized melastomataceous outgroup and the tree counting algorithm of Frolich (1987), since terminal cymose inflorescences are the strongly predominant condition within non-Miconieae melastomes. Terminal inflorescences occur in over 80% of non-Miconieae genera, and strongly predominate in all tribes except the Blakeeae Benth. & Hook. f. In addition, Weberling (1988) noted that all melastomes show monotelic inflorescences, with the basic form being a pleiothyrsoid terminating a leafy shoot. In this study the monophyly of the axillary-flowered Miconieae was accepted as a useful preliminary hypothesis and a cladistic analysis of these taxa was conducted. The results of this analysis are then used to suggest generic realignments and to reevaluate the preliminary hypothesis of monophyly of the axillary-flowered taxa.

Cladistic Analyses

METHODS

The cladistic analyses were conducted using the Wagner parsimony algorithm (with global branch-swapping and multiple parsimony options) of the PAUP (i.e., Phylogenetic Analysis Using Parsimony, Version 2.4; Swofford, 1985) package of computer software.

Fifteen Evolutionary Units (EUs) were used in most of the analyses (Table 1), based on a survey of ca. 370 herbarium specimens representing 150 species (and supplemented, where possible, by the addition of information from recent taxonomic studies). Several taxa also were studied during the course of fieldwork in Haiti, the Dominican Republic, Puerto Rico, and Jamaica. In some analyses, an additional EU representing either a generalized terminal-flowered taxon or *Clidemia* sect. *Miconiopsis* Cogn. was used. Although terminal-flowered, *Clidemia* sect. *Miconiopsis* has been considered to be related to the other sections of *Clidemia* included in this study, and its inclusion in a few analyses was designed to test this hypothesis. The inclusion of a generalized terminal-flowered taxon in some analyses was designed, in a very preliminary way, to evaluate the hypothesis that the axillary-flowered Miconieae are monophyletic. Placement of this generalized terminal-flowered taxon is considered very tentative because this EU is extremely heterogeneous, making the determination of its ancestral character states problematic (see Table 1).

Forty-two characters were used and assigned plesiomorphic (ancestral: scored as 0) and apomorphic (derived: scored as 1) states (Table 1). Apomorphic features used in the computer analyses are listed below. Nearly all characters were polarized using the Merianieae as an outgroup, with character states uniformly found (or, for a few characters, those states most commonly represented) in the out-group considered plesiomorphic (Stevens, 1980; Wheeler, 1981; Wiley, 1981; Maddison et al., 1984; Frolich, 1987). When EUs are polymorphic for a given character, an estimate of the ancestral condition was made. The states of a few characters were unknown for certain taxa, and these are scored as "missing data," indicated by a "?" in the data matrix (Table 1). Trees were rooted by using a hypothetical ancestor with all characters scored as plesiomorphic.

APOMORPHIC CHARACTERS

1. Stems quandrangular and 4-winged/ridged; plesiomorphic condition: stems ± terete. Quadrangular stems are considered an autapomorphy of *Killipia* Gleason and occur in *K. quadrangularis* Gleason (the type species). However, two other species have terete stems, and the ancestral condition within *Killipia* is not known. A coding of "0" for this EU would not affect the analyses because the feature is autapomorphic.

2. Growth pleonanthic (indeterminate); plesiomorphic condition: growth hapaxanthic (determinate). (See character 12.)

3. Megastyloid crystals present; plesiomorphic condition: only small styloids and/or druse crystals present. (See character 4.)

4. Crystals exclusively druses; plesiomorphic condition: small or large styloids and druse crystals present. The polarity of characters 3 and 4 was determined by using the Crypteroniaceae (Dahlgren & Thorne, 1984) as an outgroup (see discussion in Johnson & Briggs, 1984; Vliet et al., 1981). This family, which is closely related to the Melastomataceae, contains genera with druses and with small styloids (Baas, 1981), and this crystal complement is taken as the ancestral condition in melastomes. It is likely that megastyloids have evolved in a few lineages (sometimes with the loss of druses), while styloids have been lost in other lineages, resulting in druses being the only crystal type in those groups. That styloids and druses are known from more distantly related families of Myrtales, such as Myrtaceae and Combretaceae (Vliet & Baas, 1984) supports this polarity. Variation in crystal complement within the Merianieae is poorly known.

5. Elongate multicellular hairs absent; plesio-

TABLE 1. Character divergence values for taxa used in cladistic analyses. Taxon names abbreviated by first four letters of genus name, except *Henriettea* (HENT), *Henriettella* (HENL), *Clidemia juruensis* (CJUR), generalized terminal-flowered taxon (TERM). An asterisk indicates that the opposite state occurs in some species of that taxon; a question mark indicates that the character state is in doubt or unknown.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
MECR	0	1	0	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0*	0	0	1	0	0	0	0	0	0	0	1	0	0
SAGR	0	1	0	1	0	0	0	0	0*	0	0	1	0*	1	1	0	1	0	1	0	0	0	0	0	0*	0	0	0	0*	0*	0	0	0	0	0	0	0	0	0	1	0	0
KILL	1*	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	?	?
PENT	0	1	0	1	0	0	0	0	0	0	0	1	0*	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0*	0	0	0	0	0	0	0	0	0	1	?	?
HUIL	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?
MAIE	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0?	0?
CALO	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	?
CJUR	0	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	?
HENT	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0*	0	0	0	0	0	0	0	0	0	0	0*	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0
HENL	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0*	0	1	0	0	0*	0	0	0	0	0*	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0
LLEW	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	?	?
KIRK	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0*	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	?	?
LORE	0	1	1	0	0*	0	0	0	0	0	0	1	0*	0	0	0*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1*	0	0	1	0	0	0	1	0	1	0	1
BELL	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1*	0	0	1	0	0	0	1	0	1	0	1
MYRI	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1
MICO	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	?	?
TERM	0	0	0	1	0*	0	0	0	0*	0*	0	0	0	1	0*	0*	0*	0*	0*	0	0*	0	0*	0	0	0*	0	0	0*	0	0*	0	0	0	0	0	0	0	0	1	0	0

morphic condition: elongate multicellular hairs present, often strigose. *Mecranium* Hook. f. and *Killipia* are unique in lacking a well-developed indumentum. A few species of *Loreya* DC., e.g., *L. ovata* Berg ex Triana, *L. arborescens* (Aublet) DC., and *L. nigricans* Triana, lack such hairs as well. Renner (in press) hypothesized the loss of strigose hairs to be a synapomorphy of a species group within *Loreya*. Thus, the presence of such hairs is considered the ancestral condition within the genus.

6. Multicellular hairs elongate with radiate to stellate-globular basal portion (or clearly derived types); plesiomorphic condition: multicellular hairs various, but not as above. This distinctive hair morphology is much modified (see discussion, and Judd, 1986b) in a few species, but such extremes are connected by intermediate types, sometimes even on the same plant.

7. Multicellular hairs minute, globular, and unbranched to irregularly branched and matted (not strigose); plesiomorphic condition: multicellular hairs various but not as above. This character is limited to *Mecranium* (including *Ekmaniocharis* Urban) and *Ossaea acuminata* DC. The feature is important in determining that *Mecranium* spp., *Ossaea acuminata*, and *Ekmaniocharis crassinervis* Urban form a monophyletic group but does not help in inferring relationships among the EUs.

8. Multicellular hairs conspicuously stellate (with stalk and elongated arms); plesiomorphic condition: multicellular hairs various but not as above. In these analyses this feature is considered an autapomorphy of *Clidemia* sect. *Miconiopsis*. Very similar hairs occur in many terminal-flowered species, e.g., *Miconia* sects. *Jucunda* (Cham.) Naudin and *Tamonea* (Aublet) Cogn.

9. Leaves clearly anisophyllous; plesiomorphic condition: leaves isophyllous or nearly so. A few specialized species of *Clidemia* sect. *Sagraea* (DC.) Cogn. have anisophyllous leaves. The isophyllous condition is considered ancestral within *Clidemia* sect. *Sagraea*, following a preliminary analysis of variation within the group.

10. Leaves with pair of pouchlike formicaria at base of blade; plesiomorphic condition: leaves lacking formicaria. Similar ant-domatia that occur in terminal-flowered taxa, e.g., *Tococa* Aublet, *Clidemia* D. Don, *Myrmidone* Mart., probably evolved independently (see discussion). *Ossaea bullata* (Pilger) Gleason, possibly a member of the *Sagraea* group, has been reported to possess similar formicaria (Whiffin, 1972).

11. Cuticle of abaxial leaf epidermis papillose; plesiomorphic condition: epidermis nonpapillose. Renner (in press) pointed out that this feature correlates well with cuticle thickness and suggested that the character has important ecological consequences.

12. Inflorescences axillary (in leaf axils or at nodes on old wood); plesiomorphic condition: inflorescences terminal. Terminal cymose inflorescences (as discussed above) occur in over 80% of genera within non-Miconieae melastomes. Thus, proliferating inflorescences (in which the terminal axis returns to vegetative growth, producing axillary buds that develop vegetative branches instead of flower-bearing paracladia—see Weberling, 1988) are considered derived. The process of proliferation results in a vegetative shoot in which the flowers are borne in axillary cymose paracladia. Delayed anthesis of the paracladia can even result in cauliflory.

13. Inflorescences fasciculate; plesiomorphic condition: inflorescences cymose. Although fascicles occur in a few species of *Loreya*, *Clidemia* sect. *Sagraea* (including axillary, 4-merous species of *Ossaea* DC.), and the 5-(6-)merous species of *Ossaea*, cymose inflorescences are considered to be the ancestral condition in these groups. Renner (in press) also considered fasciculate inflorescences to be derived within *Loreya*.

14. Flowers more or less sessile; plesiomorphic condition: flowers pedicellate.

15. Flowers 4-merous; plesiomorphic condition: flowers other than 4-merous. (See character 16.)

16. Flower parts frequently more than 5; plesiomorphic condition: flowers 4- or 5-merous. Generally, 5-merous flowers are considered primitive, with higher and lower floral numbers treated as derived. *Henriettea* DC. and *Loreya* contain a few species with numerical plans greater than five, while *Henriettella* Naudin and *Kirkbridea* Wurdack contain a few species with 4-merous flowers. Within each of these genera, 5-merous flowers are considered ancestral. Renner (in press) considered floral numbers greater than five to be derived and used this feature to link some species of *Loreya* with *Bellucia* Raf. The ancestral condition in *Kirkbridea* is in doubt; however, recoding the state of this EU as "1" for this character does not change the topology of the discovered cladograms.

17. Flowers small; plesiomorphic condition: flowers moderate to large.

18. Hypanthium strongly ribbed; plesiomorphic condition: hypanthium nonribbed. This character is an autapomorphy of *Clidemia* sect. *Calophysoides* Cogn.

19. External calyx lobes more or less conspicuous and well developed; plesiomorphic condition: external calyx lobes absent or inconspicuous.

20. External calyx lobes absent; plesiomorphic

condition: external calyx lobes present. Some species of *Henriettella* have lost external calyx lobes independently of the loss in *Loreya*, *Bellucia*, and *Myriaspora* DC. This was determined because it is evident that *Henriettella* evolved out of a group within *Henriettea*, which has external calyx lobes.

21. Internal calyx lobes very elongate and closely associated with external lobes; plesiomorphic condition: internal calyx lobes not elongate, variously developed but not closely appressed to internal lobes. This feature is an autapomorphy of *Killipia*.

22. Internal calyx lobes connate into a membranous, dome-shaped, apiculate cap that ruptures irregularly at anthesis; plesiomorphic condition: internal calyx lobes free. This character is an autapomorphy of *Mecranium* (including *Ekmaniocharis*). Although *Ossaea acuminata* has somewhat caplike calyx lobes, they are only partially connate. The internal calyx lobes are free and imbricate at their extreme apices. This species is included within the *Mecranium* EU since it has the other apomorphies of this clade (characters 7, 19, and 32; see discussion).

23. Internal calyx lobes circumscissilly dehiscent (and noncalyptrate); plesiomorphic condition: internal calyx lobes more or less persistent, or if circumscissile, then calyptrate. This character is considered an autapomorphy of *Clidemia* sect. *Miconiopsis*, although a similar condition is seen in *Miconia* sects. *Tamonea* and *Jucunda* (a group included within the generalized terminal-flowered taxon).

24. Buds closed, with thick triangular calyx lobes that cover bud up to the final stage prior to anthesis (and sometimes fused into a cap); plesiomorphic condition: buds open, calyx lobes of variable shape and thin, the petals exposed much before anthesis. This feature is an autapomorphy of *Bellucia*.

25. Internal calyx lobes reduced to a more or less smooth rim; plesiomorphic condition: internal calyx lobes clearly evident. This is a noninformative character (see Table 1) because it is found only in a few derived species within *Henriettella* and *Clidemia* sect. *Sagraea*.

26. Internal calyx lobes fused into a conical, apically closed calyptra and conspicuously strigose; plesiomorphic condition: internal calyx lobes noncalyptrate (or if so, then not as above). This is an autapomorphy of *Myriaspora*.

27. Internal calyx lobes fused into an apically open cap (opening into sepal-like segments or circumscissilly); plesiomorphic condition: internal calyx lobes noncalyptrate (or if so, then not as above). This feature is limited to *Llewelynia* Pittier and a few (probably related) species of *Henriettea* (see discussion).

28. Calyx a cap open at apex and falling off by circumscissile slit; plesiomorphic condition: calyx not open-calyptrate, or if so, then opening by longitudinal slits into triangular sepal-like segments. This character is an autapomorphy of *Llewelynia* and is a further specialization of character 27.

29. Petals narrowly triangular and more or less acute at apex; plesiomorphic condition: petals ovate to elliptic (or obovate) with blunt to more or less acuminate apices. Preliminary analyses of variation within *Mecranium* (including *Ekmaniocharis*) and *Clidemia* sect. *Sagraea* (including axillary, 4-merous species of *Ossaea*) have led to the conclusion that ovate to elliptic petals with more or less acuminate to blunt apices constitute the ancestral condition within these groups. Obovate petals have evolved within a group of *Mecranium* species. It is noteworthy that *Ossaea acuminata*, a narrow-petaled species, is a sister species to *Mecranium amygdalinum* (Desr.) C. Wright in Sauv., a fairly blunt-petaled species (Skean, in prep.).

30. Petals with a dorso-apical tooth; plesiomorphic condition: petals lacking a dorso-apical tooth. This feature occurs in a few species of *Clidemia* sect. *Sagraea* (including the species of *Ossaea* with axillary, 4-merous flowers) and in the 5- or 6-merous species of *Ossaea*. A scoring of "1" for this character in these two EUs does not alter their placement in relation to the very different *Henriettea* group.

31. Petals usually pubescent, sometimes only with very few hairs near apex; plesiomorphic condition: petals glabrous (or with a single apical hair). Hairs on the petals have been lost in a few species of *Loreya* and *Bellucia*.

32. Androecial fringe present; plesiomorphic condition: androecial fringe absent. This feature is a strong and consistent synapomorphy of *Mecranium* species, including *Ekmaniocharis crassinervis* and *Ossaea acuminata*.

33. Anthers with two well-developed dorso-basal projections; plesiomorphic condition: anthers various but lacking two well-developed dorso-basal projections.

34. Anthers usually robust and fleshy, opening by one or two minute pores; plesiomorphic condition: anthers not robust and fleshy, various.

35. Anther sacs basally bifurcate, i.e., sagittate; plesiomorphic condition: anther sacs not bifurcate at base.

36. Anther sacs more or less wrinkled; plesiomorphic condition: anther sacs smooth. The best expression of this feature is in *Maieta* Aublet.

37. Stamens numerous, i.e., more than twice

the number of petals; plesiomorphic condition: stamens twice the number of petals. This is an autapomorphic character of *Llewelynia*.

38. Stigma very conspicuously and radiately ridged; plesiomorphic condition: stigma not radiately ridged.

39. Placenta highly divided; plesiomorphic condition: placenta undivided or nearly so. This is an autapomorphy of *Myriaspora*.

40. Fruit a berry; plesiomorphic condition: fruit a capsule.

41. Chromosome number of $n = 28$; plesiomorphic condition: $n = 17$ (or 15, 20). (See character 42.)

42. Chromosome number of $n = 15, 20$; plesiomorphic condition: $n = 17$ (or 28). The terminal-flowered Miconieae were used as a generalized outgroup for the determination of polarity of the incompletely known characters 41 and 42.

RESULTS

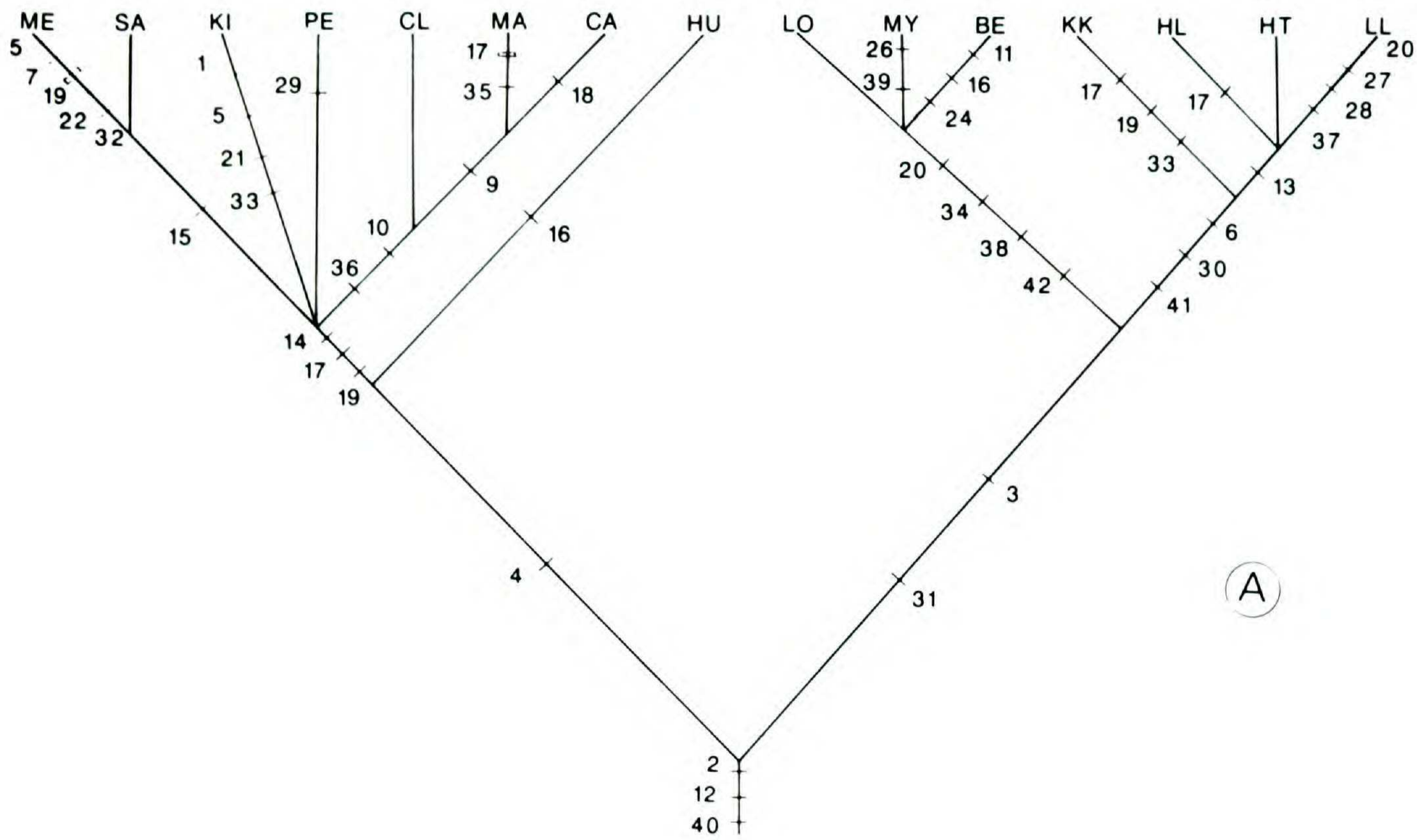
Initial computer runs using the entire data set for the 15 axillary-flowered EUs resulted in the discovery of 100+ equally parsimonious trees (but only 15 different topologies when multi-furcations are taken into account), all with a length of 28 steps and a consistency index of 0.714 (or 48 steps and consistency index of 0.813 when autapomorphies and uniform characters were included). The strict consensus tree resulting from this analysis is presented in Figure 1B. In addition a tree indicating character state changes is presented (Fig. 1A). This tree is preferred due to its pattern of character variation, especially the linking of *Mecranium* and *Clidemia* sect. *Sagraea* on the basis of 4-merous flowers (15), and the linking of *Henriettea*, *Henriettella*, and *Llewelynia* on the basis of fasciculate inflorescences (13). The relationships of the EUs representing *Loreya*, *Bellucia*, *Myriaspora*, *Henriettea*, *Henriettella*, and *Llewelynia* did not vary in any of the trees generated by PAUP. In addition, *Kirkbridea* consistently linked with *Henriettea*, *Henriettella*, and *Llewelynia*, in some trees as the cladistically basal member of this clade, in others as the sister group of *Henriettella*. In all trees, the EUs representing *Maieta*, *Clidemia* sect. *Calophysoides*, and *Clidemia juruensis* (Pilger) Gleason were always joined, and *Huilaea* Wurdack was always the basal member of the clade representing taxa with only druse crystals. Thus the large number of generated trees is due to the numerous possible topologies among the remaining EUs in the analyses, i.e., *Mecranium* (including *Ekmaniocharis* and *Ossaea acuminata*), *Clidemia* sect. *Sagraea* (including *Necramium* Britton and axillary 4-merous species of *Ossaea*), *Killipia*, and *Pentossaea*, here described to include the axillary-flowered, 5-merous (or less commonly 6-merous) species of *Ossaea*.

Thus, several analyses were conducted using just those EUs possessing only druse crystals (i.e., top eight EUs listed in Table 1) with characters not pertaining to this complex deleted. These analyses generated 45 equally parsimonious trees (but comprising only seven different tree topologies) of 11 steps and with a consistency index of 0.727 when all characters were weighted equally (or of 25 steps and a consistency index of 0.880 when autapomorphies and uniform characters were included). However, when the apomorphy of 4-merous flowers was stressed (weighted by 2, as seems reasonable, since this character is quite uniform within EUs under investigation), only 15 trees (representing only two topologies) were produced, all with 12 steps and a consistency index of 0.750 (or of 26 steps and a consistency index of 0.889 when autapomorphies and uniform characters were included). The consensus tree resulting from the analysis in which all characters are weighted equally is identical to that produced in the analysis of all axillary-flowered taxa (Fig. 1B). Both cladograms resulting from the weighted-character analysis are given in Figure 1C and D.

When an EU representing a generalized terminal-flowered taxon is included in the analysis, over 100 equally parsimonious trees were found, all with a length of 32 steps and a consistency index of 0.688 (or of 50 steps and a consistency index of 0.780 when autapomorphies and uniform characters were included). These trees are very similar to those generated in the analyses involving only axillary-flowered taxa (Fig. 1), and the four different topologies involving their basal branches are presented in Figure 2, illustrating the various positions of the genus *Huilaea* and a generalized terminal-flowered taxon. When *Clidemia* sect. *Miconiopsis* (another taxon producing terminal inflorescences) is included in the analysis, many trees are again generated (of 55 steps and a consistency index of 0.745, including autapomorphies), all linking this entity with either *Killipia* or a clade containing *Killipia*, *Clidemia* sect. *Sagraea*, and *Mecranium*.

DISCUSSION

The cladograms presented in Figures 1 and 2 indicate that the axillary-flowered Miconieae are divided into two major clades. The first is composed of those taxa containing megastyloids (3) in their leaf and stem tissues (often with druse crystals as well) and usually possessing slightly pubescent petals (31). The group also generally has distinctly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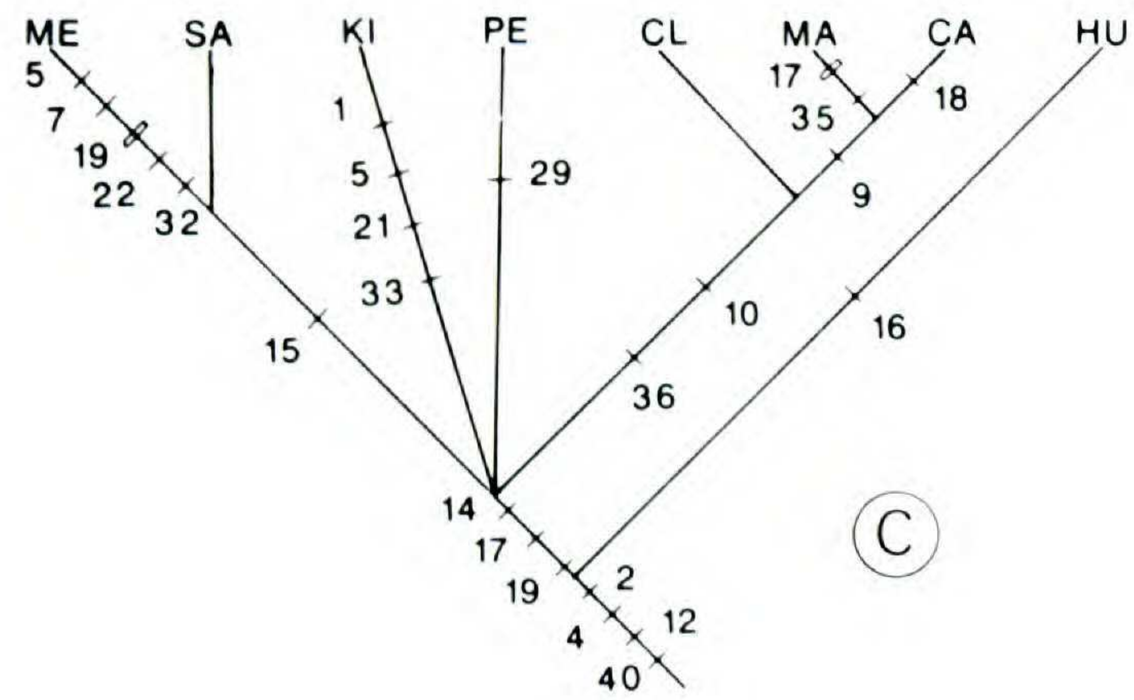
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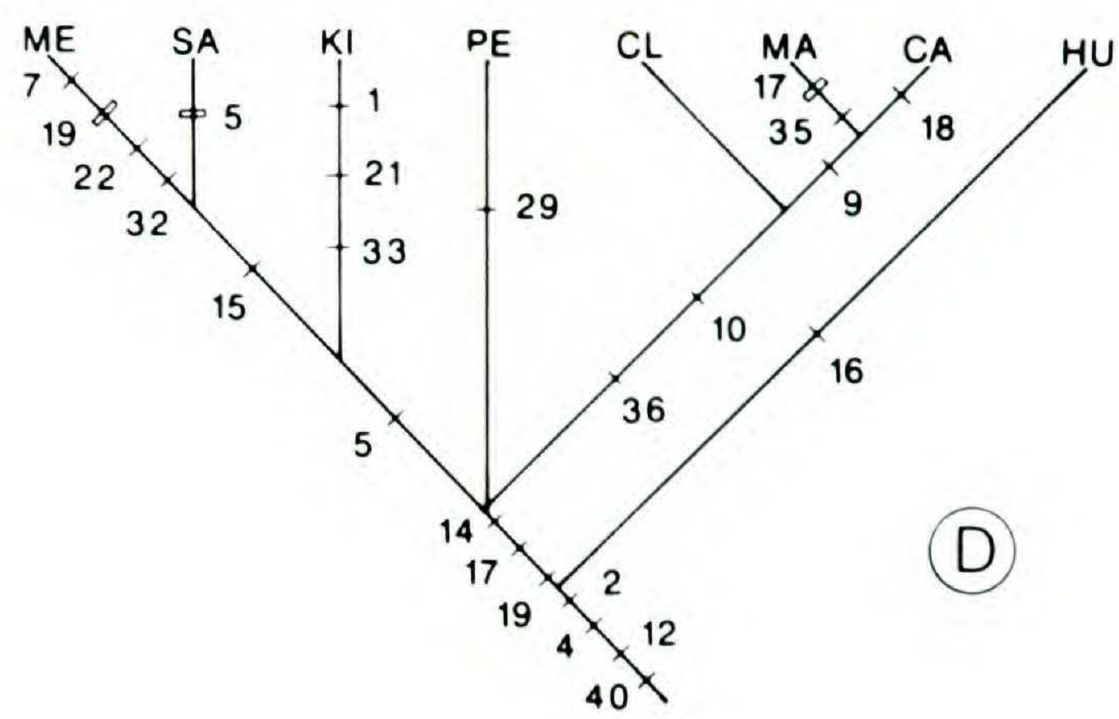
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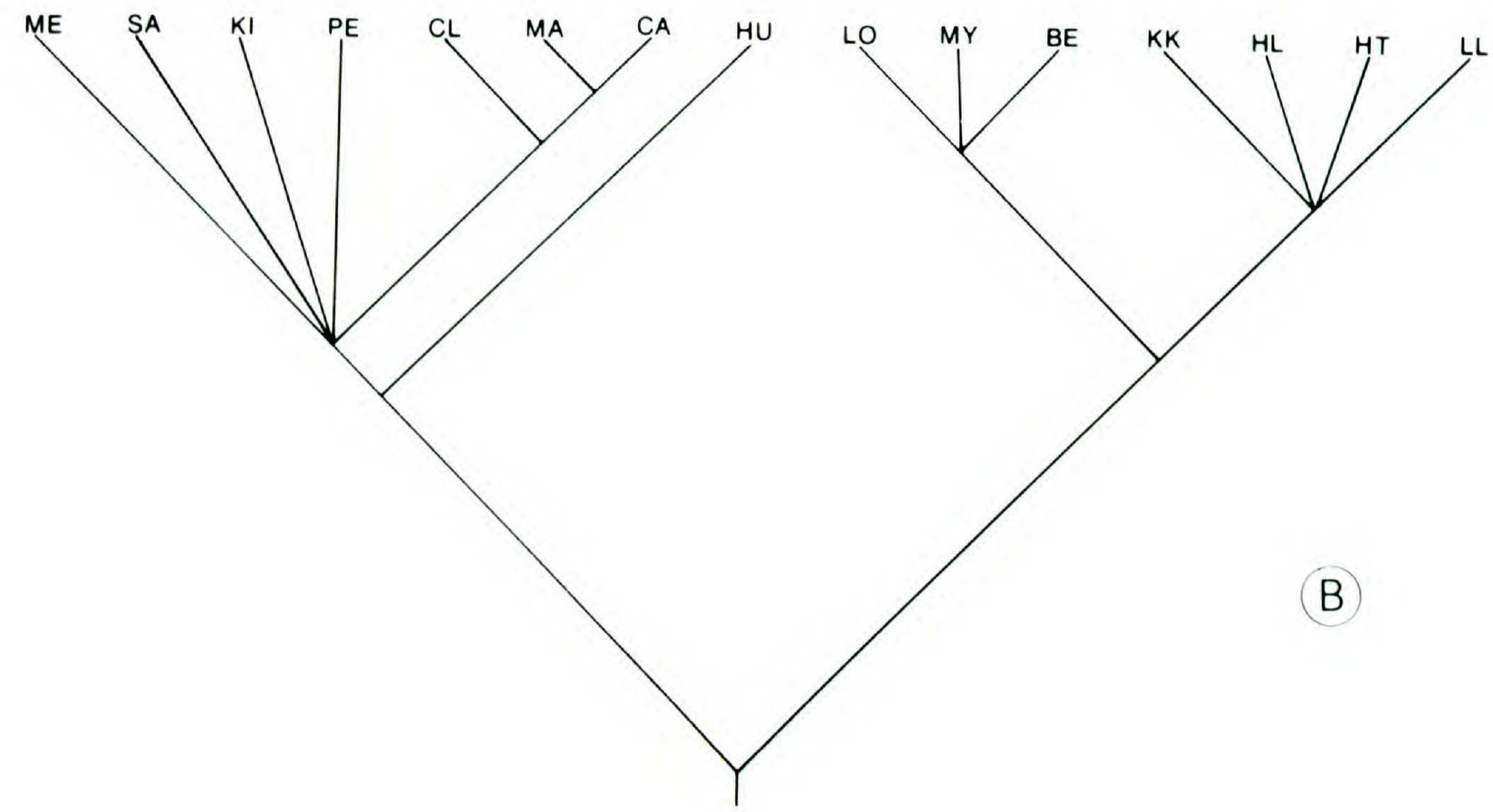
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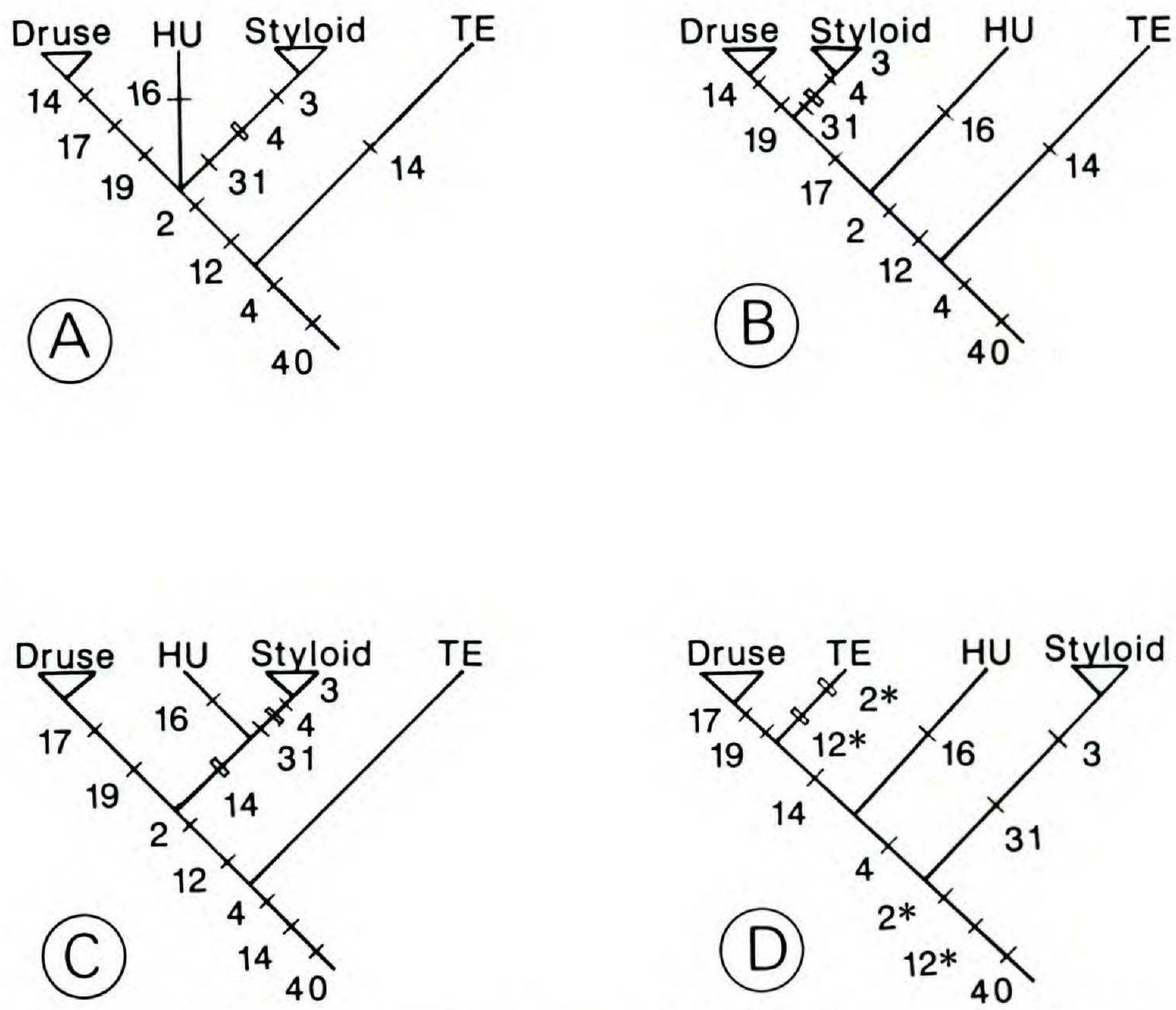

FIGURE 2. Basal portion of cladograms resulting from analysis of axillary-flowered taxa and generalized terminal-flowered taxon, all of 50 steps, consistency index = 0.78. Reversals indicated by open bars. Taxon abbreviations: *Huilaea* (HU), exclusively druse-containing group (Druse), megastyloid-containing group (Styloid), and generalized terminal-flowered taxon (TE). *These characters could also have evolved independently in basal members of megastyloid- and druse-containing lineages (see text).

pedicellate flowers. This clade may be divided into two clearly marked subgroups based on vegetative and reproductive characters. *Loreya*, *Bellucia*, and *Myriaspora* are united by the synapomorphies of flowers lacking external calyx lobes (20), possessing robust fleshy anthers (34), an expanded and radiately ridged stigma (38), and a chromosome number of $n = 15$ or 20 (42). In contrast, *Henriettea*, *Henriettella*, *Llewelynia*, and *Kirkbridea* form a clade based upon the presence of multicellular strigose hairs with a stellate, radiate, irregularly branched, or suprabasally expanded base, or hair types clearly modified from these conditions (6), petals with an apical apiculum on the abaxial surface (30), and a chromosome number of $n = 28$ (where known, 41). *Kirkbridea* likely is cladistically basal in this group, with *Henriettea*, *Henriettella*, and *Llewelynia* being united by the additional synapomorphy of fasciculate inflorescences (13). (It should be noted that parallelism in flower size (17) occurs within these genera, which is not surprising considering the variability of this feature within the tribe. Linking *Kirkbridea* and *Henriettella* on the basis of this character is considered implausible.)

The remaining taxa included in the analysis form a second clade based on the following synapomorphies: presence of only druse crystals in leaf and stem tissues (4), small more or less sessile flowers (17, 14), and usually well-developed external calyx lobes (19). The extremely isolated genus *Huilaea* probably is basal within this clade (Fig. 1A, B) because it shows only the synapomorphy of exclusive presence of druse crystals (4), having large and clearly pedicellate flowers. The relationships among the taxa comprising this clade are not well resolved. However, it is clear that *Maieta*, *Clidemia* sect. *Calophysoides*, and *C. juruensis* form

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FIGURE 1. Cladograms resulting from PAUP analyses.—A. Preferred tree resulting from analysis of all axillary-flowered taxa, 48 steps, consistency index = 0.813.—B. Consensus tree.—C, D. Cladograms resulting from PAUP analyses of taxa containing only druse crystals—two 26-step trees generated in analysis weighting character 15; topology C equals consensus tree of this analysis. Reversals indicated by open bars; taxa abbreviated by first two letters of generic or sectional name, except *Henriettea* (HT), *Henriettella* (HL), and *Kirkbridea* (KK).

a monophyletic group based on the presence of morphologically very similar pouchlike ant-domatia (formicaria) at the base of the leaf blade (10) and wrinkled anthers (36). In addition, *Maieta* and *Clidemia* sect. *Calophysoides* have anisophyllous leaves (9). If the character of 4-merous flowers is stressed, then *Mecranium* is probably most closely related to *Clidemia* sect. *Sagraea*, and the two may be linked by this feature (15). Linking *Killipia* with *Sagraea* and *Mecranium* in some trees on the basis of the shared loss of strigose hairs (5) probably has little phylogenetic significance.

The terminal-flowered taxa of Miconieae may be a paraphyletic or monophyletic group basal to all the axillary-flowered taxa (Fig. 2A–C) or a possible sister taxon to the taxa containing only druses (Fig. 2D). In the first alternative, the axillary-flowered condition evolved just once and serves as a synapomorphy of all axillary-flowered Miconieae; in the second, axillary arrangements are hypothesized to have evolved in the druse and megastyloid clades independently (or, less likely, evolved in the stem lineage of the entire tribe with a reversal to terminal cymes occurring in the ancestor of *Miconia* and relatives). The possible polyphyly of the axillary-flowered Miconieae clade will be investigated more thoroughly in a later paper. It is certainly possible that *Miconia* and relatives are more closely related to the axillary-flowered "druse-containing" genera than initially hypothesized.

When an EU representing a generalized terminal-flowered taxon is included in the analysis, the position of *Huilaea* in the cladograms becomes more variable than in the initial analyses (compare Figs. 1 and 2). This variability may reflect the presumed phylogenetic isolation of this genus. It seems more reasonable to link *Huilaea* with *Mecranium*, *Clidemia* sect. *Sagraea*, *Maieta*, and *Killipia* on the basis of the presence of only druse crystals in its tissues (4) than with *Loreya*, *Henriettea*, and *Kirkbridea* on the basis of a reversal to pedicellate flowers (14) (Fig. 2).

The presence of both terminal and axillary flowers in *Clidemia* sect. *Miconiopsis* (Cogniaux, 1888, 1891) is not surprising (see Judd, 1986a, for discussion of similar variation evident in *Miconia*, especially in sects. *Octomeris* (Naudin) Benth. & Hook. and *Tamonea*; and Troll, 1964, and Weberling, 1965, 1988, for more general discussion of inflorescence structure and position). Wurdack's suggestion (pers. comm.) that this group is closest to *Miconia* is likely correct. Note especially the similarity in stellate indumentum (8; Fig. 4) and circumscissilly dehiscent calyx (23). The section may be quite close to *Miconia* sects. *Tamonea* and *Jucunda*. The linking of *Clidemia* sect. *Miconiopsis* with *Killipia* or a clade containing *Killipia*, *Clidemia* sect. *Sagraea*, and *Miconia* in the cladistic analysis probably is due to homoplasy in several fairly weak characters, e.g., loss of strigose hairs (5), or to several potential synapomorphies between the axillary-flowered taxa containing only druse crystals and *Miconia* (and relatives), e.g., more or less sessile flowers (14) or well-developed external calyx lobes (19).

In spite of the necessarily preliminary nature of these cladistic analyses, their results help determine the previously confused generic limits within this difficult tribe (see also Judd, 1986a, b). In interpreting these results, I have attempted to delimit monophyletic and phylogenetically equivalent genera within the tribe that are recognizable on the basis of several morphological characters. Thus *Huilaea*, *Mecranium* (including *Ekmaniocharis* and *Ossaea acuminata*), *Killipia*, *Maieta* (including *Clidemia* sect. *Calophysoides* and *C. juruensis*), *Loreya* (including *Bellucia* and *Myriaspora*), *Henriettea* (including *Henriettella* and *Llewelynia*), and *Kirkbridea* are considered to be generically distinct. In addition, *Clidemia* sect. *Sagraea* (including *Necramium* and the species of *Ossaea* with axillary 4-merous flowers) is recognized at the generic level. Finally, the species of *Ossaea* with axillary 5- (or 6-)merous flowers are in need of generic recognition and are described herein as *Pentossaea*. The systematics of each of these taxa is discussed briefly below.

Discussion of axillary-flowered genera. *Loreya* is clearly delimited by its distinctive usually robust fleshy anthers (34), expanded and radiately ridged stigma (38), lack of external calyx lobes (20), and range of chromosome numbers (42, see Solt & Wurdack, 1980). The group possesses megastyloids in its leaf and stem tissues (pers. obs.; Baas, 1981) and is clearly monophyletic. However, if *Bellucia* and *Myriaspora* are segregated as separate genera, the result is a paraphyletic *Loreya* (Fig. 1). *Bellucia* is characterized by papillose abaxial leaf cuticle (11), closed buds (24), i.e., the buds have thick calyx lobes that cover the buds up to the final stage prior to anthesis (and are even fused into a cap in a few species, e.g., *Bellucia dichotoma* Cogn. and *B. acutata* Pilger), and tendency for floral merosities greater than five (16) (see Renner, in press). In contrast, *Myriaspora* is characterized by its highly divided placentae (39), calyx lobes fused into an unusual cap (26, which is probably not homologous with the cap of some species of *Bellucia*), and long hairs on the abaxial

surface of its petals. In addition, *Myriaspora* produces inflorescences in the leaf axils (as do several species of *Bellucia*), while the usual condition in *Loreya* is to have the inflorescences lateral on leafless nodes below the leaves; it should be noted, however, that this character is often variable within a genus (Judd, 1986a; Renner, in press).

No autapomorphies are evident for *Loreya* when certain species are segregated as either *Bellucia* or *Myriaspora* (Fig. 1). The paraphyly of *Loreya* is made even more apparent when it is realized that *Loreya subrotundifolia* (Wurdack) S. Renner and *L. riparia* S. Renner link with *Bellucia* on the basis of higher numbers of floral parts and that *L. mespiloides* Miq., *L. spruceana* Benth. ex Triana, and *L. klugii* S. Renner link with *Myriaspora* on the basis of testa characters and one-pored anthers (Renner, in press).

Thus, recognition of *Bellucia* and *Myriaspora* distorts the best estimate of phylogenetic structure currently available for this group of species. Their recognition is also doubtful on purely phenetic grounds, since the patristic distances separating *Bellucia* and *Myriaspora* from the cladistically related taxa within a narrowly delimited *Loreya* are comparable to those separating other clades within *Loreya* (Renner, in press). Thus, as is characteristic of traditional taxonomic procedure (see Stevens, 1984, 1986), recognition of *Bellucia* and *Myriaspora* can only be justified by selective weighting of certain features (in this case the characters of cuticular papillae, bud structure, placental form, and inflorescence position) due to their supposed greater ecological significance. I see no reason to weight these characters more than any others used in these analyses. The decision to recognize a broadly circumscribed *Loreya* is not new; Baillon (1877) also considered *Bellucia* and *Loreya* congeneric (although only few species were known to him), and Macbride (1941: 497) considered this treatment "preferable it seems . . . to 'straining at a gnat' to keep them apart." Gleason (1932) considered the genera only "weakly separated"; however, they were maintained as distinct by Wurdack (1973, 1980) and Renner (in press).

Henriettea is easily recognized by its usually fasciculate inflorescences (13), distinctive indumentum of elongate multicellular hairs with an expanded, radiate to globular-stellate basal portion (or easily derived types, such as stellate-hairs, peltate-scales, elongate hairs with numerous small mainly basal projections, elongate hairs with a suprabasal expanded region and a narrowed basal attachment, or hairs very reduced, e.g., *Henriettella caudata* (DC.) Naudin, *H. glabra* Cogn.; see Wurdack, 1986) (6), petals with a minute dorso-apical apiculum (30), and chromosome number of $n = 28$ (41, Solt & Wurdack, 1980). Fasciculate inflorescences have evolved independently in a few species of *Loreya* (Renner, in press), and the inflorescences of *Henriettea squamulosa* (Cogn.) W. Judd have reverted to a pedunculate condition (Judd, 1986b). *Henriettea* is clearly monophyletic and shows the presence of calcium oxalate megastyloids (similar in structure to those of *Loreya*) in its leaf and stem tissues (pers. obs.; see also Welle & Mennega, 1977; Welle & Koek-Noorman, 1981; Baas, 1981).

As with *Loreya*, problems of paraphyly occur when *Llewelynia* and *Henriettella* are recognized as distinct from *Henriettea* (Fig. 1). *Llewelynia* is phenetically distinctive (Pittier, 1939; Wurdack, 1973) and easily recognized by its loss of external calyx lobes (20), open calyx cap that opens by a circumscissile slit (27, 28), and numerous stamens (37), while *Henriettella* is only marginally separable due to its smaller flowers (17) and tendency to have shorter anthers that open by larger, gaping pores (see Wurdack, 1973, 1980). A nearly obsolete internal calyx has evolved in a few species of *Henriettella*, e.g., *H. sessilifolia* (L.) Triana, and in many species the internal calyx lobes are not well developed. *Henriettea* and *Henriettella* were considered congeneric by Macbride (1941: 500), who stated that "there seems to be no significant concomitance of the characters of petals, anthers or pubescence that have been used to maintain two similar but distinct genera." He added that "the characters moreover often exist in degrees of development." Richard A. Howard also will consider *Henriettea* and *Henriettella* to be congeneric in his Lesser Antilles flora (pers. comm.). Wurdack (1972: 418) maintained these genera but noted that "a generic transition zone exists between *Henriettella ovata* Cogn. and *Henriettea patrisiana* DC., with *Henriettella parviflora* (Griseb.) Triana perhaps not distinct from the latter."

The genera differ in flower size, anther characters, and indumentum, but intermediates exist. Not surprisingly, there are no autapomorphies for *Henriettea* when defined narrowly, and its species certainly intergrade with *Henriettella*.

The floral buds of some other species of *Henriettea* (e.g., *H. spruceana* Cogn., *H. succosa* (Aublet) DC., *H. stellaris* Berg ex Triana, and *H. ramiflora* (Sw.) DC.) possess an expanded and open cap formed by the inner calyx lobes very similar to (and likely homologous with) that of *Llewelynia*, although opening longitudinally rather than cir-

cumscissilly. These species are likely basal members of the clade leading to *Llewelynia*. It is of interest that Wurdack (1973) suggested a similarity in general facies between *Llewelynia* and *Henriettella*, and Welle & Koek-Noorman (1981) reported similarity in wood anatomical characters between *Llewelynia* and *Henriettella*. It thus seems best to recognize a broadly defined, and monophyletic *Henriettea* by including both *Henriettella* and *Llewelynia* within it.

Kirkbridea clearly is related closely to *Henriettea* s.l. (Fig. 1). *Kirkbridea* (Wurdack, 1976) is quite distinctive due to its pedunculate inflorescences and anthers with two well-developed dorsobasal projections (33). *Kirkbridea* and *Henriettea* show variation in number of floral parts.

Huilaea is evidently very isolated, as Wurdack (1957, 1976) suggested at the time of his description of the genus. It clearly is distinct generically and is recognizable due to its pendent, three-flowered cymose inflorescences with very long peduncles and large, clearly pedicellate, 6-merous flowers.

Maieta, defined broadly, is a monophyletic group best recognized by its characteristic pouchlike formicaria at the base of its leaf blades (10) (Fig. 3; see discussion of morphology, development, and ecological functions of these structures in Gleason, 1931; Schnell, 1967; Whiffin, 1972; Neto & Asakawa, 1978; Benson, 1985). It should be noted that ant-domatia of various types undoubtedly have evolved independently in a few to many species of several other genera (e.g., *Sagraea* DC., *Tococa*, *Clidemia*, *Henriettea*, and *Conostegia* D. Don), and additional developmental studies are necessary in order to determine appropriate homologies of such structures within the tribe. The presence of structurally and positionally very similar pouchlike ant-domatia is accepted as a provisional synapomorphy of *Maieta* s. str. and *Clidemia* sect. *Calophysoides* until such developmental investigations are conducted. The group also tends to have slightly wrinkled anthers (36) and clearly anisophyllous leaves (9). Druses are the only crystals known in this group. The species of *Maieta* (defined narrowly—see Aublet, 1775; Wurdack, 1980) have sagittate anthers (35) and show a reversal toward large flowers (17), while those of *Clidemia* sect. *Calophysoides* have a distinctly ribbed hypanthium (18). Both, along with possibly a few other species of *Clidemia*, such as *C. juruensis*, are considered congeneric. The close relationship between these species of *Clidemia* with pouchlike formicaria and the phenetically similar species of *Maieta* has long been recognized. Macbride (1941: 479) remarked that "*Clidemia* remains . . . a concept rather arbitrarily retained but conveniently so on account of *Maieta* (in which Baillon, Hist. Pl. 7: 56. 1880 rightly merged it) being the older name." I agree and here consider *Maieta* to be congeneric with *Clidemia* sect. *Calophysoides* (and *C. juruensis*).

Killipia (Fig. 4) is a distinctive genus not easily confused with any other in the complex of genera possessing only druse crystals. Noteworthy apomorphies are the very long internal calyx lobes with closely associated external calyx lobes (21) and distinctive anthers with two dorso-basal projections (33); see description of genus in Gleason (1925). The stems of *Killipia quadrangularis* are quadrangular and ridged-winged (1); however, two other species have terete stems. The abaxial leaf surface of *K. quadrangularis* is usually red, an apomorphy not included in the analysis, which has also evolved within several genera with terminal inflorescences. The cladistic relationships of *Killipia* are obscure, although it is closest to *Maieta*, *Mecranium*, *Sagraea*, and *Pentossaea* (Fig. 1).

The species formerly of *Ossaea* with axillary 5-merous or occasionally 6-merous flowers warrant generic recognition (Fig. 5). The petals of this group are narrowly triangular with an acute apex (29), and the group is clearly separable from related taxa (see key). It is not surprising that a group of *Ossaea* species was found to be in need of generic recognition, since the genus has long been suspected of being polyphyletic (see Judd, 1986a). Wurdack (1962: 206), for example, stated that "the genus is an artificial assemblage of various species groups." The distinctive clade, with axillary 5-(6-)merous flowers, is here described as the genus *Pentossaea*.

Pentossaea W. Judd, gen. nov.

Genus novum, *Sagraea* DC. affine, a quo floribus 5-meris (vs. 4-meris), petalis semper anguste triangularibus, apicibus acutis differt. TYPE SPECIES: *Pentossaea brachystachya* (DC.) W. Judd.

Evergreen subshrubs or shrubs with pleonanthic shoots; twigs ± terete, nodose, glabrous to densely strigose, with a ridge encircling each node; druse crystals present. Indumentum of conspicuous, unbranched, slender to stout, strigose, multicellular hairs with or without glandular apices and of minute, multicellular, glandular hairs (or sometimes glandular-stellate hairs) occurring on stems, leaves, inflorescence axes, and hypanthia, or in some species ± restricted to reproductive parts. Buds narrowly ovoid, sylleptic, usually densely pubescent. Leaves

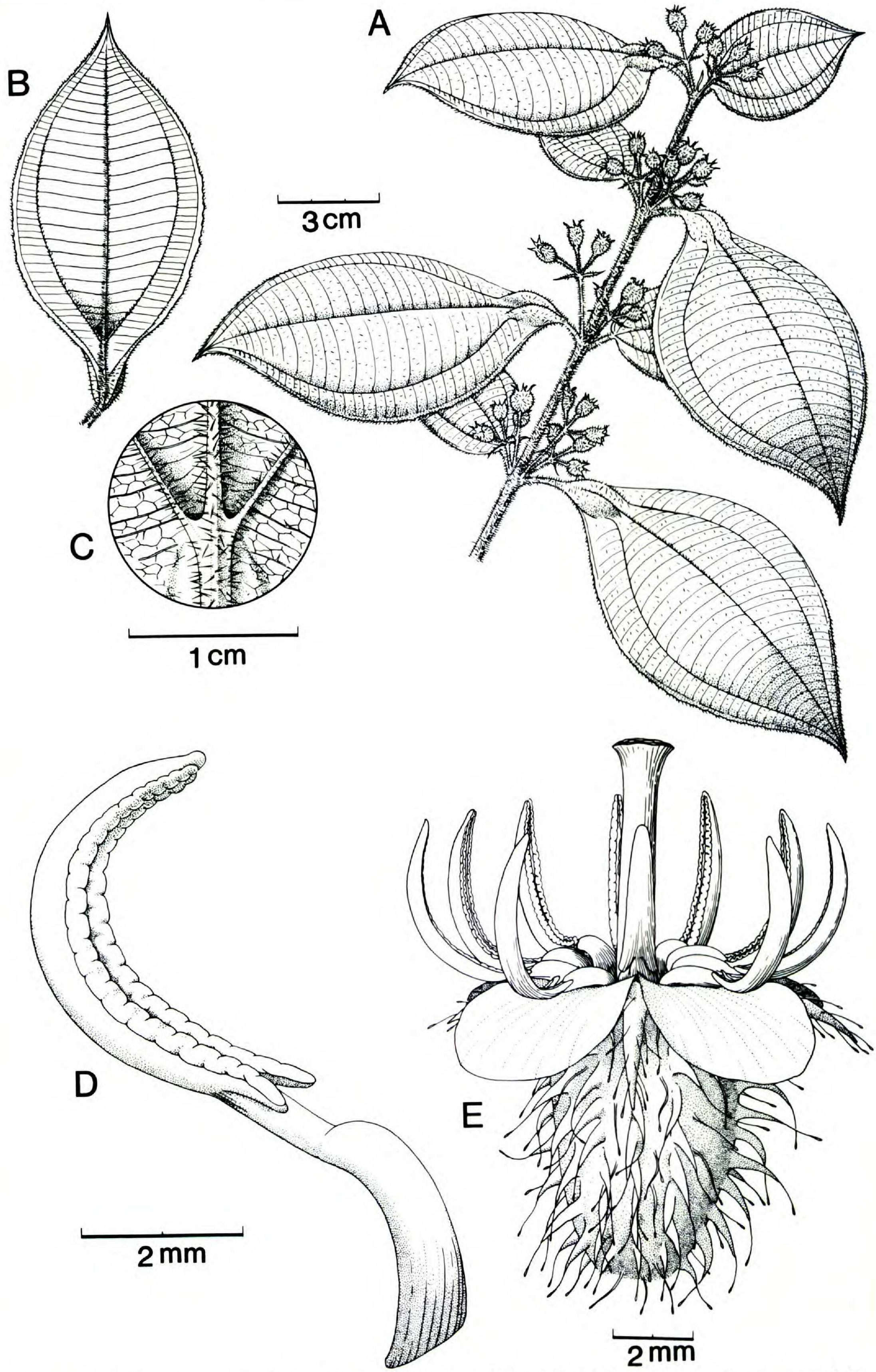

FIGURE 3. *Maieta poeppigii* Mart. ex Cogn.—A. Habit.—B. Leaf, abaxial view showing formicaria.—C. Detail showing entrance to formicaria.—D. Stamen.—E. Flower.

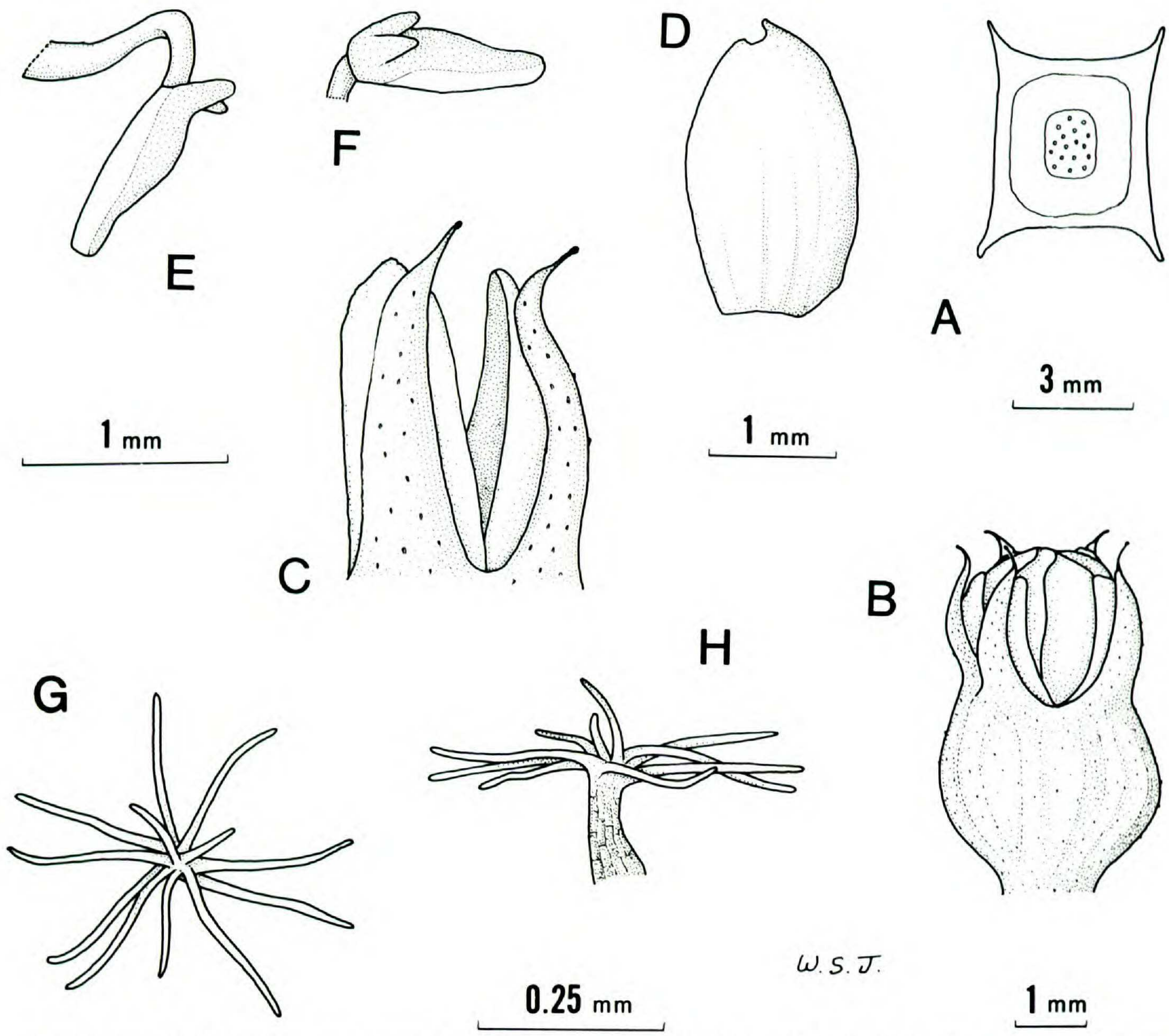

FIGURE 4.—A–F. *Killipia quadrangularis*. A. Stem, section. B. Flower bud. C. Calyx lobes. D. Petal. E, F. Stamens.—G, H. *Clidemia kappleri* Cogn., stellate hairs.

opposite, decussate, petiolate to nearly sessile, estipulate, herbaceous to coriaceous, ± plane; adaxial surface essentially glabrous (at maturity) or sparsely to densely covered with unbranched, elongate, multicellular hairs and sometimes also with minute glandular hairs (especially in vein impressions or at petiole junction); abaxial surface usually sparsely to densely covered with slender to stout, unbranched, elongate, multicellular hairs along with minute glandular to glandular-stellate, multicellular hairs (i.e., glandular hairs unbranched or sparsely branched with one branch glandular and the others nonglandular), sometimes only with glandular hairs and becoming ± glabrous with age; domatia not observed in vein axils; margin serrate in distal ca. ¾ of lamina to entire, plane to slightly revolute near base, the teeth ending in an elongate multicellular hair (and often associated with additional elongate hairs); venation acrodromous, slightly suprabasal, with a prominent midvein, 1–4 pairs of secondary veins (1 of these often intramarginal and inconspicuous), numerous percurrent tertiary veins ± perpendicular to midvein and reticulate to orthogonal quaternary and higher-order veinlets; petiole caniculate, essentially glabrous to densely strigose-pubescent. Inflorescences axillary cymes (occasionally reduced and ± fasciculate) borne in the leaf axils and in a few species on leafless nodes below the leaves, usually borne singly, rarely 2 per axil, bracteate, with opposite, narrowly triangular to ovate or oblong bracts (the 2 lowest protecting the inflorescence in bud and quickly caducous). Flowers perfect, 5- or 6-merous, sessile. Hypanthium ± cylindrical, abaxially with conspicuous, unbranched, elongate hairs with or without glandular apices, intermixed with minute glandular or glandular-stellate hairs, adaxially glabrous or with a few hairs around apex. External calyx lobes 5 or 6, conspicuous, elongate, terete. Internal calyx lobes 5 or 6, distinct (noncalyptrate), ± triangular, with obtuse, acute, to acuminate apices. Petals 5 or 6, ± white, narrowly triangular with acute api-

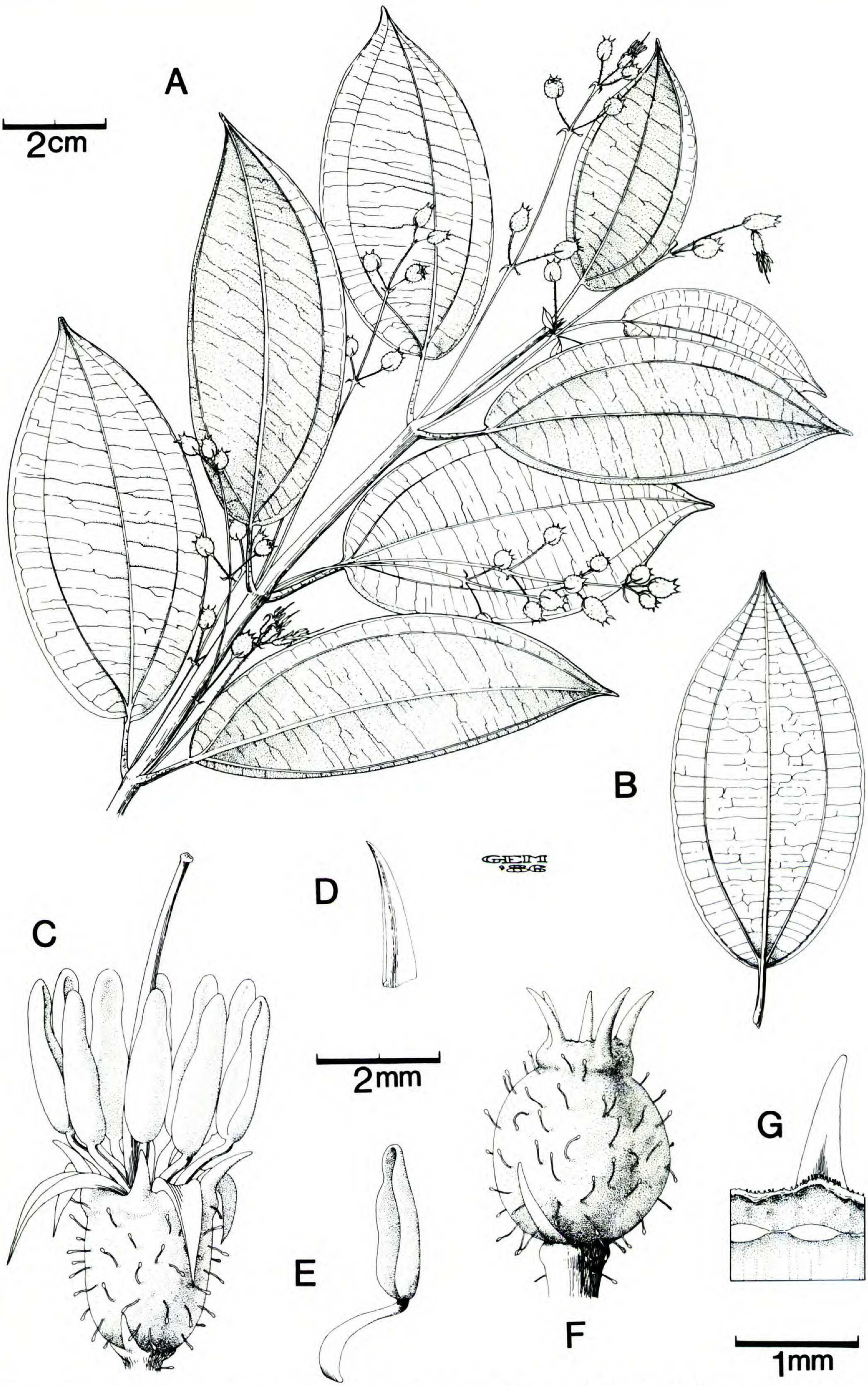

FIGURE 5. *Pentossaea coriacea.*—A. Habit.—B. Leaf.—C. Flower.—D. Petal.—E. Stamen.—F. Berry.—G. Calyx and inner surface of hypanthium; note absence of androecial fringe.

ces, 1-veined, glabrous or occasionally with a single dorso-apical projection (hair), rarely with a few glandular hairs. Stamens 10–12, ± isomorphic, glabrous, geniculate, inserted at apex of hypanthium, androecial fringe lacking; filament narrowly ovate to oblong, flattened dorsally; anther narrowly ovate to oblong, sometimes slightly curved, the 2 anther sacs dehiscing confluently by means of a single small apical pore, the connective sometimes slightly prolonged beyond the bases of the anther sacs. Ovary inferior or nearly so, 3–5-locular, with axile placentation and numerous ovules, the apex occasionally prolonged into several blunt appendages surrounding the style. Style cylindrical, ± straight; stigma capitate, papillose. Berries red to blue, with indumentum similar to hypanthium. Seeds small, rounded- to angular-obovate, the testa smooth to slightly roughened.

Pentossaea angustifolia (DC.) W. Judd, comb. nov. *Leandra angustifolia* DC., Prodr. 3: 154. 1828.

Pentossaea brachystachya (DC.) W. Judd, comb. nov. *Clidemia brachystachya* DC., Prodr. 3: 156. 1828.

Pentossaea confertiflora (DC.) W. Judd, comb. nov. *Clidemia confertiflora* DC., Prodr. 3: 156. 1828.

Pentossaea congestiflora (Naudin) W. Judd, comb. nov. *Clidemia congestiflora* Naudin, Ann. Sci. Nat. Bot., Ser. 3, 17: 344. 1852.

Pentossaea coriacea (Naudin) W. Judd, comb. nov. *Clidemia confertiflora* DC., Prodr. 3: 156. 1828.

Pentossaea heteronervis (Naudin) W. Judd, comb. nov. *Sagraea heteronervis* Naudin, Ann. Soc. Nat. Bot., Ser. 3, 18: 98. 1852.

Pentossaea marginata (Desr.) W. Judd, comb. nov. *Melastoma marginata* Desr. in Lam., Encycl. 4: 32. 1797.

Additional new combinations will certainly become necessary following a detailed revision of the genus.

The axillary-flowered 4-merous species of *Ossaea* and the very similar species traditionally placed in *Clidemia* sect. *Sagraea* (also axillary-flowered and 4-merous; see Cogniaux, 1891) are typically separated by the technical character of apically acute vs. blunt petals. However, I found this character to vary continuously within the group, and several species placed in *Clidemia* sect. *Sagraea* actually have acuminate or acute petals (e.g., *C. oligantha* Urban, *C. fuertesii* Cogn., *C. domingensis* (DC.) Cogn., *C. crossosepala* Griseb.), while others treated in *Ossaea* may have blunt-tipped petals (e.g., *O. barahonensis* Urban & E. Ekman or *O. setulosa* Urban). Some taxa have been considered members of both groups by various authors. In addition, phenetically very similar species have sometimes been placed in the two "genera," e.g., *Clidemia crossosepala* and *Ossaea hirtella* (Sw.) Triana (see Adams, 1972), and petal shape and apex occasionally vary infraspecifically, as in *Clidemia fuertesii*. Thus, all 4-merous, axillary-flowered members of the "druse-containing group" (Fig. 2) with free internal calyx lobes, no androecial fringe, and a usually well-developed strigose indumentum are placed together in *Sagraea* (Fig. 6; also see key).

Necramium (Britton, 1924), a genus with 4-merous axillary flowers having ovate, sharply acuminate petals and with an indumentum of long strigose hairs and irregularly branched-stellate hairs, clearly also belongs to this clade. A close association between *Necramium* and some species of *Ossaea* was recognized by Wurdack (1973: 721–722), who stated that *Necramium* was "realmente bien acomodado dentro de *Ossaea* DC. sensu Cogniaux pero la necesidad por una transferencia posterior cuando ese conjunto artificial se disperse se opone a la sinonimización inmediata." Wurdack (pers. comm.) suggested affinity of *Necramium* to *Ossaea* sect. *Octopleura* (Griseb.) Cogn. This is judged unlikely, however, since the latter group has terminal inflorescences (although frequently deflexed to a seemingly lateral position, see Judd, 1986a), a glandular dorso-basal connective appendage, and strongly costate fruits.

Necramium (Britton, 1924) is not the oldest name available for this clade, the names *Ossaea* and *Sagraea* (de Candolle, 1828) both having priority. Because the types of *Sagraea* (*S. capillaris* (Sw.) DC., here designated) and *Ossaea* (*O. scalpta* (Vent.) DC., here designated) fall within the group circumscribed above, and the two genera were described at the same time (de Candolle, 1828), either name is available for this group. The name *Sagraea* is chosen here, since I wish to avoid the use of *Ossaea*, a name that has been used for a great many discordant species-groups (see Wurdack, 1962, 1973, and Judd, 1986a). It is noteworthy that Triana (1871) considered these axillary-flowered species (along with a few discordant elements) to be generically separable (as *Sagraea*) from the terminal-flowered *Clidemia*.

Sagraea may be most closely related to *Mecranium*, a more specialized genus also showing 4-merous flowers, this a potential synapomorphy (15, Figs. 1, 2). *Sagraea* is considered to be metaphyletic (Donoghue, 1985; Mishler, 1985; Mishler & Brandon, 1987) because its ca. 60 species show no autapomorphies in some of the generated clado-

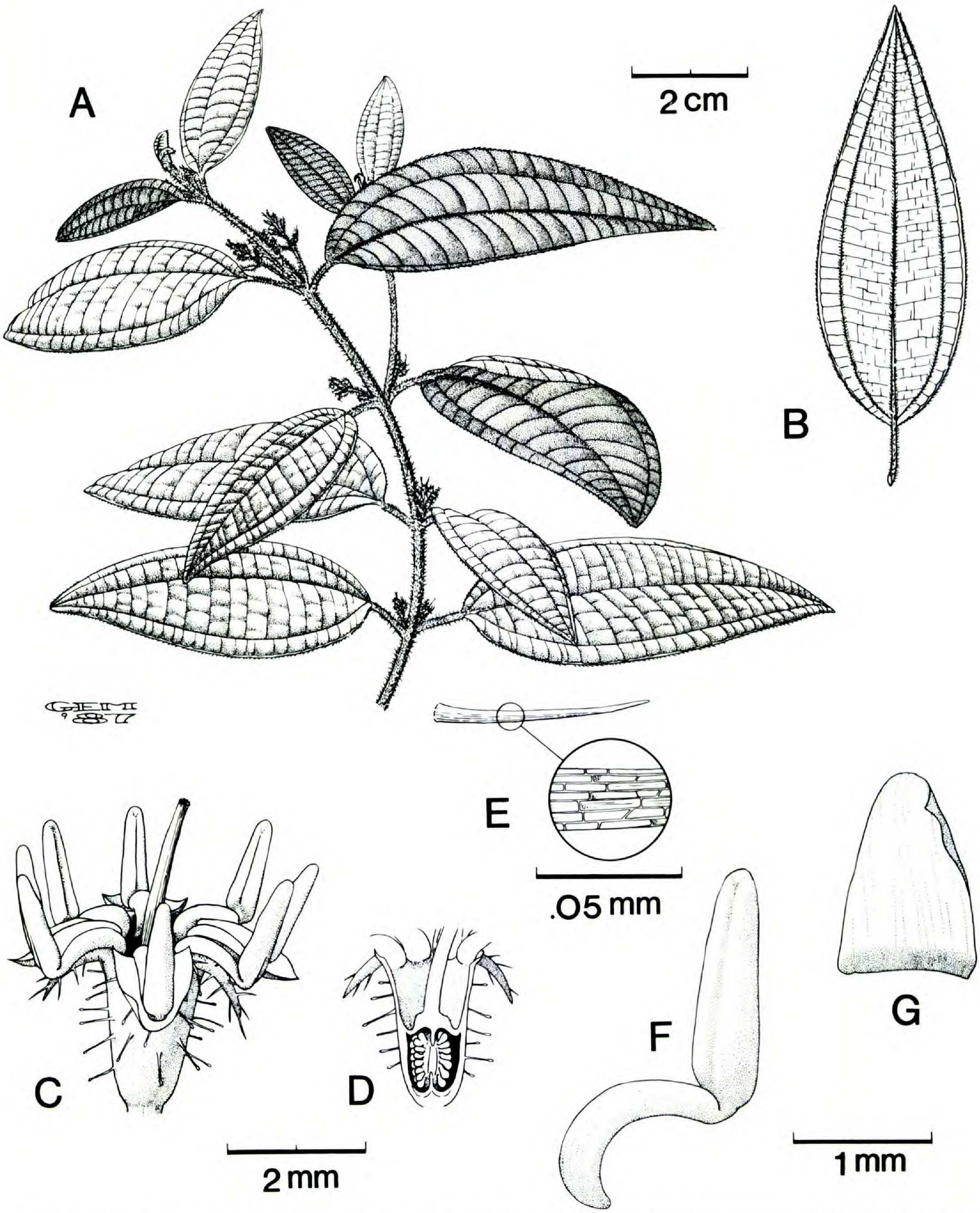

FIGURE 6. *Sagraea* (represented by the species better known as *Ossaea barahonensis*).—A. Habit.—B. Leaf.—C. Flower—D. Longitudinal section of flower showing hypanthium; note lack of androecial fringe.—E. Elongate multicellular hair.—F. Stamen.—G. Petal.

grams. However, in other equally parsimonious trees, the group appears monophyletic, being defined by a reversal to strigose hairs (5) or by a parallel evolution of 4-merous flowers (15). The group is possibly paraphyletic, but no character conclusively demonstrating this has been determined. Generic recognition of this phenetically rather variable group is considered appropriate and preferable to leaving its species in several artificially delimited genera.

Several species of *Sagraea* have evolved formicaria at the base of the petiole, e.g., *Clidemia*

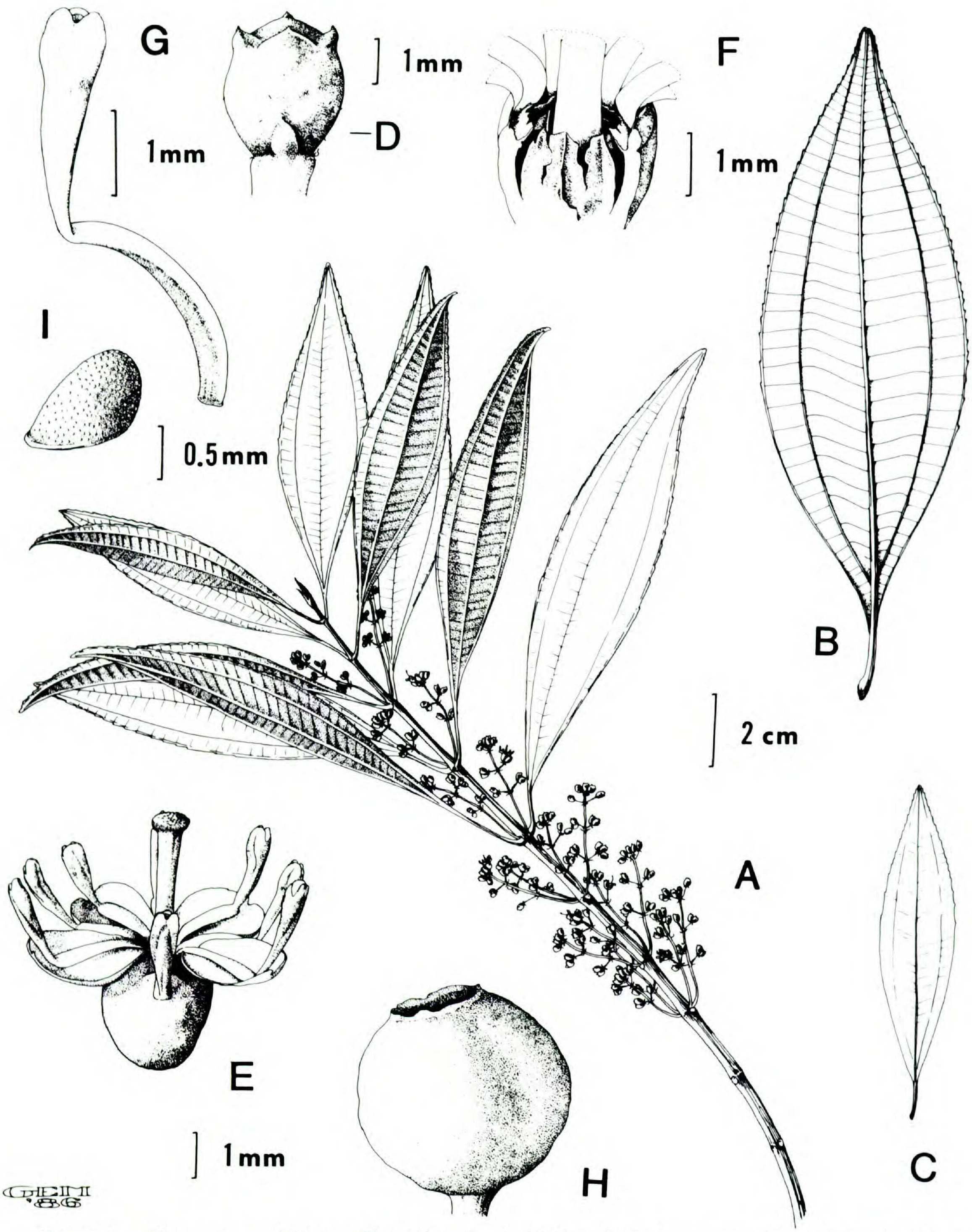

FIGURE 7. *Mecranium multiflorum* (Desr.) Triana.—A. Habit.—B, C. Leaves.—D. Flower bud.—E. Flower.—F. Hypanthium, androecial fringe, and ovary apex.—G. Stamen.—H. Berry.—I. Seed.

tococoidea (DC.) Gleason and *C. crenulata* Gleason; these species have sometimes been confused with *Maieta* (see Gleason, 1931). The structure and position of these formicaria are quite different from those of the *Maieta* and likely due to convergent evolution. Plants with a climbing habit and strongly anisophyllous leaves occur in *Clidemia epiphytica* (Triana) Cogn., a species that is also cytogenetically distinctive (Solt & Wurdack, 1980). As discussed above, anisophyllous leaves are char-

acteristic of *Maieta*, and this feature undoubtedly has evolved in parallel in the two genera.

It is not considered appropriate to make the many necessary new combinations in *Sagraea* until a thorough taxonomic revision of the genus has been completed. The species considered to belong in *Sagraea* and used in this cladistic investigation are: *Clidemia aphanantha* (Naudin) Sagot, *C. capituliflora* Cogn., *C. ciliata* D. Don, *C. crenulata* Gleason, *C. crossosepala* Griseb., *C. cursoris* Wurd., *C. discolor* (Triana) Cogn., *C. divaricata* (C. Wright ex Griseb.) Cogn., *C. domingensis* (DC.) Cogn., *C. epiphytica* (Triana) Cogn., *C. fendleri* Cogn., *C. fuertesii* Cogn., *C. graciliflora* Huber, *C. grisebachii* Cogn., *C. heteroneura* Cogn., *C. insularis* Domin (= *Sagraea capillaris* (Sw.) DC.), *C. involucrata* (Griseb.) C. Wright ex Sauv., *C. minutiflora* (Triana) Cogn., *C. monantha* L. Williams, *C. obliqua* Griseb., *C. oligantha* Urban, *C. plumosa* (Desr.) DC., *C. purpureo-violacea* Cogn., *C. pusilliflora* Cogn., *C. pycnaster* Tutin, *C. quadripetala* Almeda, *C. rubra* (Aublet) Mart., *C. rubrinervis* Cogn., *C. septulinervia* Cogn., *C. sericea* D. Don, *C. sessiliflora* (Naudin) Cogn., *C. silvicola* Gleason, *C. tococoidea* (DC.) Gleason, *C. trichotoma* C. Wright, *C. ulei* Pilger, *C. umbrosa* Cogn., *Ossaea curvipila* Urban & E. Ekman, *O. hirtella* (Sw.) Triana, *O. navasensis* Britton & Wilson, *O. nipensis* Britton & Wilson, *O. petiolaris* (Naudin) Triana, *O. rufescens* (Griseb.) C. Wright, *O. scabrosa* (L.) DC., *O. scalpta* (Vent.) DC., *O. setulosa* Urban, and *O. woodsii* W. Judd & Skean.

Mecranium (Fig. 7) is a distinctive monophyletic species group distinguished from other genera containing druse crystals by its internal calyx lobes fused into a domelike, apiculate, and membranous cap that is ruptured irregularly by elongation of the style and emergence of the petals at anthesis (22), the external calyx lobes reduced in length and often inconspicuous (reversal of 19), androecial fringe (i.e., a ring of erose to ciliate appendages arising from apex of hypanthium [torus] internal to the stamens [32]), and usually sparse and poorly developed indumentum (7); see Judd (1986a) and Skean & Judd (1986). Because these apomorphic characters are found also in the monotypic *Ekmaniocharis* (*E. crassinervis*; Urban, 1921; Judd, 1986a; Skean, in press), it is clear that this genus belongs in *Mecranium*. Likewise, *Ossaea acuminata* (Judd, 1986a) shows all these apomorphies except that of a domelike, apiculate cap. In this species the apices of the internal calyx lobes are distinct and imbricate, although the lobes are connate for most of their length, forming a structure that may be similar to the condition from which an apiculate cap was derived. It is obvious that *O. acuminata* is a basal member of the *Mecranium* clade. The nomenclatural transfers will be made by James D. Skean, Jr. in a monographic study of *Mecranium* currently near completion. A more detailed analysis of the phylogeny of this genus will be presented by Skean (in prep.).

In summary, the phylogenetic relationships (and taxonomic diversity) among the axillary-flowered Miconieae are most clearly represented by a taxonomic system recognizing the following nine genera as delimited above: *Henriettea*, *Huilaea*, *Killipia*, *Kirkbridea*, *Loreya*, *Maieta*, *Mecranium*, *Pentossaea*, and *Sagraea*.

KEY TO AXILLARY-FLOWERED MICONIEAE

1a. Plants with large elongate crystals (megastyloids) in leaf and stem tissues (easily observable with a hand lense in oblique razor blade sections); flowers usually clearly pedicellate; petals densely to sparsely pubescent abaxially, or with a few obscure hairs near apex, occasionally glabrous.
  2a. Flowers with radiately ridged, conspicuously expanded stigmas and with usually robust, fleshy anthers; indumentum of very slender to stout, elongate, unbranched, multicellular hairs ..... *Loreya*
  2b. Flowers with nonridged, less conspicuous stigmas and with nonfleshy anthers; indumentum of slender to stout, elongate, multicellular hairs with radiate to stellate-globular basal portion (or derived types, e.g., stellate hairs, peltate scales, elongate hairs with minute projections near base, or elongate hairs with a suprabasal expanded region and narrowed basal attachment).
    3a. Anthers with 2 well-developed dorso-basal projections; inflorescences clearly pedunculate ..... *Kirkbridea*
    3b. Anthers without dorso-basal projections; inflorescences usually sessile and fasciculate ..... *Henriettea*
1b. Plants with only ± spherical crystals (druses) in leaf and stem tissues, lacking megastyloids; flowers ± sessile or pedicellate; petals usually glabrous or with a single apical hair.
  4a. Flowers clearly pedicellate, i.e., pedicels ca. 1–1.5 cm long; inflorescences pendulous and 3-flowered with peduncle ca. 10–35 cm long ..... *Huilaea*
  4b. Flowers ± sessile; inflorescences various but the peduncle shorter than ca. 6 cm.
    5a. Flowers 5- or sometimes 6-merous.
      6a. Plants with pouchlike formicaria (ant-domatia) at bases of leaf blades; leaves often clearly anisophyllous ..... *Maieta*
      6b. Plants without formicaria; leaves ± isophyllous.
        7a. Petals narrowly triangular, with acute apices; plants with elongate, multicellular, un-

branched hairs (often strigose), with or without glandular tips; anthers lacking dorso-basal projections ..... *Pentossaea*

7b. Petals ovate to elliptic, with ± blunt apices; plants lacking elongate, multicellular hairs; anthers with 2 dorso-basal projections ..... *Killipia*

5b. Flowers 4-merous.

8a. Inner calyx lobes fused in a usually conspicuous, membranous dome that ruptures irregularly at anthesis; hypanthium with a ring of erose to ciliate appendages arising internally at base of stamens, i.e., an androecial fringe; indumentum usually not well developed, of minute, multicellular, globular, or unbranched to irregularly branched, and matted hairs ..... *Mecranium*

8b. Inner calyx lobes free; hypanthium lacking an androecial fringe, although occasionally with a few hairs on adaxial surface; indumentum often conspicuously strigose, almost always with elongate, branched or unbranched, multicellular hairs, often with glandular apices ..... *Sagraea*

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